A Practical Guide To The Anatomy And Physiology Of Pacific Salmon

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91-06577/

MISCELLANEOUS SPECIAL PUBLICATION 27

A Practical Guide To The Anatomy And Physiology Of Pacific Salmon

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DEPARTMENT OF THE ENVIRONMENT
FISHERIES AND MARINE SERVICE
OTTAWA 1975

In addition to the *Miscellaneous Special Publication* series, the Fisheries and Marine Service, Department of the Environment publishes the *Journal of the Fisheries Research Board of Canada* in annual volumes of monthly issues and a *Bulletin* series. These publications are for sale from Information Canada, Ottawa K1A 0S9. Remittances must be in advance, payable in Canadian funds to the order of the Receiver General for Canada.

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Canada: $2.00 — Catalogue No. Fs 4-31/27
Other Countries: $2.40 — Contract No. KF708-5-0552

Price subject to change without notice
Information Canada

Ottawa 1975

Printed by Northern Miner Press Limited

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Abstract

SMITH, L. S., AND G. R. BELL. 1975. A practical guide to the anatomy and physiology of Pacific salmon. Fish. Mar. Serv. Misc. Spec. Publ. 27: 14 p.

Fisheries workers and the general public often need or wish to locate and identify special parts of the salmon to describe abnormalities or to submit appropriate samples rather than the whole fish for examination by specialists, but there is no single document describing the gross anatomy or general functioning of Pacific salmon species. In this publication the gross anatomy of Pacific salmon is discussed and illustrated with drawings and photographs. Aspects of anatomy and physiology of special interest to fisheries biologists are emphasized, and the cardiovascular system has been examined in some detail using angiograms and rigid plastic casts of the blood system. There is only scant discussion of the anatomy of the skeleton, muscles, and nervous system. Most of the information could also apply to Atlantic salmon and to the trouts.

Résumé

SMITH, L. S., AND G. R. BELL. 1975. A practical guide to the anatomy and physiology of Pacific salmon. Fish. Mar. Serv. Misc. Spec. Publ. 27: 14 p.

Les chercheurs en pêcheries et le grand public ont souvent le besoin ou le désir de localiser ou d'identifier des parties particulières du saumon pour décrire des anomalies ou pour soumettre des échantillons appropriés plutôt que le poisson entier pour examen par des spécialistes. Cependant, il n'existe aucun document décrivant l'anatomie macroscopique ou le fonctionnement général des espèces de saumons du Pacifique. La présente publication contient une description de l'anatomie macroscopique des saumons du Pacifique, illustrée de dessins et de photographies. Les aspects de l'anatomie et de la physiologie qui présentent un intérêt particulier pour les biologistes des pêches sont soulignés, et le système cardiovasculaire est étudié en détail à l'aide d'angiogrammes et de pièces moulées en plastique rigide du système sanguin. On ne discute que brièvement de l'anatomie du squelette, des muscles et du système nerveux. Presque toute l'information s'applique également au saumon atlantique et aux truites.

Introduction

Salmonids are one of the most intensively studied, widely cultivated, extensively distributed, and avidly sought groups of fishes in the world. It is perhaps surprising, therefore, to find that there is so little basic information about the anatomy of salmonids. It is difficult to find any published illustrations of the gross anatomy of salmonids: other anatomic illustrations (often highly diagrammatic) and descriptions are widely scattered throughout the literature.

There is a need for a condensed, practically oriented collection of illustrations and concise descriptions summarizing aspects of the gross anatomy and physiology of salmonids relevant to the common needs of laboratory and field workers in fisheries biology, conservation officers, and fish culturists. This publication is designed to meet some of these needs, particularly regarding visceral and cardiovascular anatomy, and is not intended to be an anatomic treatise in the traditional style, with its implications of great detail and specialization; almost nothing is said, for example, about the skeletal, nervous, or muscular systems. We realize that in attempting to satisfy such a diverse audience we might "fall between two stools," the academic and the practical, but it seems worth the risk. Although our approach is deliberately panoramic, it is hoped the introductory literature review will assist workers in the often difficult task of finding specific information.

The material presented herein is an assemblage of original and published work but, because this is primarily just a guide to salmon anatomy and physiology, distinctions between such are not always meticulously noted. We do not pretend to present many significant new details of salmon anatomy, the principal claim to originality or uniqueness lies in the collection and presentation of the material. We will first discuss somewhat broadly the pertinent literature and then, more specifically, integrate our findings with those of others to give a composite outline of the anatomy and physiology of a "generalized" or archetype Pacific salmon that could also apply to other salmonids.

A brief glossary of common anatomic and associated terms used in this paper is given on page 13.

Discussion of Literature

Discussing the publications on the anatomy of salmonids in the usual manner of a literature review is neither practical nor appropriate because the small number of references makes useful comparisons between species almost impossible. Confirmation of detailed anatomic relationships that is commonly done by making comparisons among several authors who looked at the same species and structures is also rarely possible. Many of the papers are difficult for most readers to obtain, being scattered in old journals, minor journals, and publications in foreign languages having limited distribution and abstracting. We make no claim to being either comprehensive or exhaustive, but have selected for discussion papers that we have found useful in solving practical problems of salmonid anatomy. The text by Lagler et al. (1962) and two books in French and German by Grassé (1958) and Harder (1964), respectively, are valuable basic references.

Skeleton and Muscle

The skeleton of salmonids has probably received more attention than any other part because the skeleton has both taxonomic and evolutionary significance, and at the same time is relatively easy to prepare, store, and study. One of the earlier papers is by Agassiz and Vogt (1845) and deals with *Salmo salar* and *S. fario*. There are many good plates of the skeleton and central nervous system. Secondarily, the anatomy of visceral organs, circulatory system, and musculature is also discussed. As is characteristic of the work by the classic anatomists of the last century, the plates are beautifully done.

Two more recent papers investigated the skeleton as a possible means of determining racial origin of Pacific salmon captured on the high seas. The monograph by Vladykov (1962) emphasizes the caudal and head skeleton of Pacific salmon. The discussion is lengthy and detailed because subspecies differences were being investigated and there are excellent photographs and drawings. The second paper by Hikita (1962) concerns the taxonomy of the genus *Oncorhynchus* in a somewhat broader sense. The general external features of each species were described and illustrated at several ages and, in addition, the skeletal anatomy was studied. Used in combination, these two references should leave few questions unanswered about general skeletal anatomy.

In contrast to skeletal anatomy, the anatomy of the musculature of salmonids has hardly been examined. Perhaps the apparent lack of specialization of muscles, except as related to the paired fins and mouth structures, was not intriguing to anatomists in comparison with the musculature of the land vertebrates. Thus, except for some discussion of muscle anatomy in the more general works such as Agassiz and Vogt (1845), the only paper we found that exclusively discussed muscular anatomy of Pacific salmon was by Greene and Greene (1914). Unfortunately, there are relatively few pictures and some are of very poor quality of reproduction, so that the paper is of less value than it might have been. There are additional general anatomy references noted below, but one that is particularly useful for indicating the manner of attachment and orientation of muscles is that for the yellow perch by Chaisson (1966).

Body Cavity (Coelom)

Illustrations of the internal organs of salmonids are suprisingly rare. Parker and Haswell (1963), *A Textbook of Zoology*, features *Salmo fario* as an example of a typical teleost fish. The authors show details of the head, tail, pectoral girdle, brain, eye, auditory organ, and show best the general visceral anatomy. Even so, they show nothing of the nerves or blood vessels supplying specific organs or regions.

Additional discussion and illustrations of the visceral anatomy are scattered through Harmer and Shipley (1904), who, in turn, cite earlier German authors (not reviewed by us) as the original source of the information. Their approach is comparative and aimed at describing the evolutionary progressions seen in fish, and the fact that some of the organs illustrated belong to salmonids is mostly incidental to the main theme of the text.

The urogenital system of salmonids has been a continuing source of problems in naming and in determining the derivation of the associated membranes and ducts (Parker 1943; Bell and Bateman 1960). The naming problem stems from the desire to apply the term cloaca (or urogenital sinus) to fish in the same way that it is applied to higher vertebrates. This is not correct, however, because the vent, genital, and urinary openings all reach the exterior of the body separately and in that order (anterior to posterior), the latter two occurring at the end of the urogenital papilla. Few bony fishes and no salmonids can be compared directly with higher vertebrates and so, for example, vent rather than anus is the term used in this paper to avoid the cloaca/anus controversy.

There has long been considerable difference of opinion about whether or not ripe ova are shed via oviducts. Kendall (1920) disputed earlier claims that ripe ova were first shed into the body cavity and stated that "inasmuch as the ova do not naturally fall into the abdominal cavity and cannot be extruded if they are displaced into it, it

follows that their adventitious presence there cannot be of advantage to the fish." More recently, Henderson (1967) claimed that "peritoneal or mesovarial folds are the structures which Kendall has termed oviducts" and that the "peritoneal folds are not functional gonaducts." "When ripe, the ova are discharged from the gonads directly into the abdominal cavity and pass through a constriction in the posterior abdominal wall into a cavity that opens to the exterior through an orifice on the urogenital papilla." We seem to have returned then to the opinion long held by many fisheries biologists that ripe eggs are first released into the body cavity before being shed. Perhaps what is missing in this seemingly incomplete explanation of the discharge mechanism of ripe sex products is knowledge of possible coordinated muscular contractions that direct the flow of eggs or sperm out of the body cavity.

There is no discrete pancreas, but insulin-secreting pancreatic tissue ("islets") is scattered mainly in the fatty layers around the pyloric caeca. The structure and function of the endocrine pancreas of fishes is discussed by Epple (1969) and Brinn (1973). Papers in the latter volume discuss other endocrine organs of bony fishes.

There is another important gland, just barely visible in the body cavity, that is not mentioned elsewhere in this paper. The ultimobranchial gland is seen as a white streak and, perhaps, a slight bulge in the transverse septum between the liver and the pericardium. It produces the hormone, calcitonin, that lowers the level of blood calcium, an important function when the fish is in sea water (Pang 1973). Salmon may provide a significant commercial source of calcitonin, because salmon calcitonin is effective in humans (Copp 1969).

The gall bladder, which may be found collapsed and almost invisible, or distended with yellowish-green bile, is situated on the inner surface of the liver where the lobes fold around the anterior part of the muscular stomach.

Cardiovascular and Lymphatic Systems

There seems to be no previously published illustration of the general organization of the circulatory system of any salmonid. However, parts of the general blood supply were illustrated by Harmer and Shipley (1904), and the circulation in certain regions and organs was elucidated by Grodzinski (1931, 1946, 1947) and his colleagues (Swienty 1939; Gorkiewicz 1947; Koniar 1947). The heart has received special attention (Randall 1968), although usually in a general article such as the comprehensive review on the circulatory (cardiovascular) system of fishes by Randall (1970). Our study of cardiovascular anatomy began with the limited objective of locating suitable sites for sampling blood (Smith and Bell 1964) and eventually encompassed the problems of interpreting the characteristics of blood in relation to its location in the circulatory system. Other physiologists have also found it necessary to work out the circulatory anatomy involved in the functions being studied, e.g. the relationship between the pseudobranch and the choroid (correctly, but uncommonly, "chorioid") gland (Hoffert et al. 1971), and the regulation of respiratory blood flow in the gills (Davis 1971) also involve anatomic considerations. An excellent comprehensive review on the structure and function of the fish gill has been published by Hughes and Morgan (1973). Thus, knowledge of the cardiovascular system can be characterized as a patchwork of information about certain regions.

The lymphatic system, on the other hand, considered to be of evolutionary significance, at least as far as knowing whether it was present or not, has been looked for in a variety of fishes. The lymphatic system of bony fishes has been described by Harmer and Shipley (1904) as being either mostly axial or mostly peripheral, with salmonids being of the peripheral type. This situation was confirmed by Wardle (1971) and reviewed for bony fishes in general by Kampmeier (1970). This does not mean tha the lymphatic system in salmonids is well understood, however, since there is sti considerable discussion over such basic points as where it connects to the venou system, for example.

Nervous System (Including Urophysis)

It appears that no one has examined the whole nervous system of salmon fro an anatomic point of view but mostly from a limited aspect in relation to a particula function (Bernstein 1970). The study of the caudal neurosecretory system (urophysis is an example of this fragmentary interest. The urophysis is an endocrine orga somewhat like the pituitary. It produces hormones in a similar manner and th hormones influence the role of the kidney tubules in particular and a variety o other osmoregulatory organs in general. In many fish the organ is readily seen as lobe or downward bulging of the spinal cord near the tail. In salmonids, however, th system is incorporated into the spinal cord and makes only a faint, if any, bulge in th shape of the spinal cord. Obvious differences in gross structure make no apparen difference in function (Fridberg and Bern 1968; Berlind 1973).

The older papers that dealt with general anatomy illustrated the brain, but no the peripheral nerves (Agassiz and Vogt 1845; Harmer and Shipley 1904; Parker and Haswell 1963). The autonomic (formerly called "sympathetic") portion of the nervou system is barely known to exist (Bernstein 1970; Campbell 1970). But since th nervous systems of vertebrates as a whole bear strong resemblances to each other many useful extrapolations can be made from the better known species to salmonids Some insight into the limitations to be expected from these kinds of extrapolation can be gained by reading such papers as the review on forebrain function by Aronson (1967). The small degree of anatomic difference to be expected within closely relate species that show widely different behavior is discussed by Rao (1967).

Early Development

The anatomy of early stages of animals can often provide considerable insight into the anatomy of the adults. Further, an understanding of the embryological development is an important part of culturing the organism. Four salmonids have been investigated in this regard: Atlantic salmon, *Salmo salar* (Battle 1944); steelhead (rainbow) trout, *S. gairdneri* (Wales 1941; Knight 1963); chinook salmon, *Oncorhynchus tshawytscha* (Riddle 1917); and chum salmon, *O. keta* (Mahon and Hoar 1956). Of the four papers, Battle's seems most complete and useful from the anatomic point of view.

Materials and Methods

Since methods and techniques are of minor importance in the context of this paper, only brief descriptions are given, and further details may be obtained from the references.

Specimens were obtained in the Pacific northwest and the species included sockeye (red) salmon *(Oncorhynchus nerka)*, coho (silver) salmon *(O. kisutch)*, and chinook (king, spring) salmon *(O. tshawytscha)*.

Much of the anatomic information was obtained by ordinary dissection of both fresh or formalin-preserved specimens. Some fresh specimens were injected with latex, usually through a cannula in the dorsal aorta, before formalin preservation, while others were dissected without treatment.

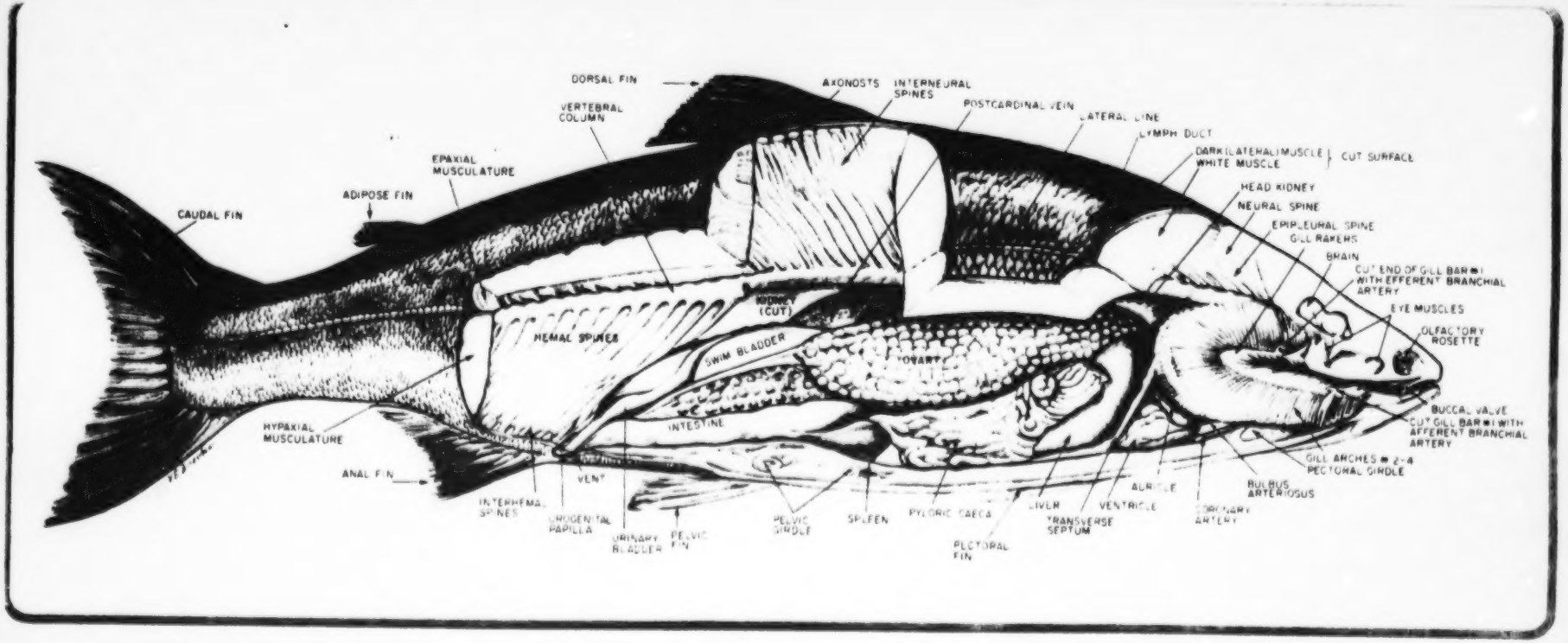


FIG. 1. Semi-diagrammatic drawing of an adult, female salmon, with portions cut away, showing the location and identity of various external and internal features.

To prepare rigid casts of the vascular system, the tail of an anesthetized, heparin-injected fish was cut off, the blood drained, and polyethylene tubes inserted into the dorsal aorta and caudal vein in the hemal arch at the cut surface. Colored solutions of polymerizing vinyl acetate were injected under steady mechanical pressure, then the whole fresh fish was corroded in concentrated KOH for 1–3 days leaving only a few soft bones and a rigid plastic "corrosion cast" of parts of the circulatory system. These vinyl casts were sometimes pruned to expose the major blood vessels.

In other preparations, fish were injected as above or into various body spaces with X-ray contrast media and then X-ray plates made. Contrast media are fluids containing substances with elements of high atomic number (e.g. iodine, barium) that are dense to X-rays and therefore make a "shadow." Radiograms of specimens whose blood vessels have been injected with contrast medium are called angiograms.

Details of the latex and resin-casting techniques are provided by Tompsett (1970), and of the radiographic techniques by Bell and Bateman (1960); Smith and Bell (1964); and Bell and Smart (1964).

Descriptions of Anatomic Features

General Gross Anatomy

The general anatomy of a typical Pacific salmon, particularly the visceral organs, is shown in Fig. 1 and 2. Figure 1 contains parasaggital sections that show most of the internal organs largely undisturbed, while Fig. 2 is a view nearly on the median plane and shows longitudinal sections of several of the organs.

The two figures illustrate a number of the typical features of the anatomy of salmonids. The kidney is the most dorsal organ in the visceral cavity and contains the postcardinal vein. The swimbladder is immediately ventral to the kidney, putting the fish's center of buoyancy below the center of gravity (which is why it turns belly-up when unconscious and the righting reflexes for the lateral fins cease to function). The esophagus is short, broad, and strong and is the site where the pneumatic duct to the swimbladder opens (not illustrated). The intestine ("gut") is surrounded anteriorly by pyloric caeca opening into the midgut, and then makes a single loop before passing

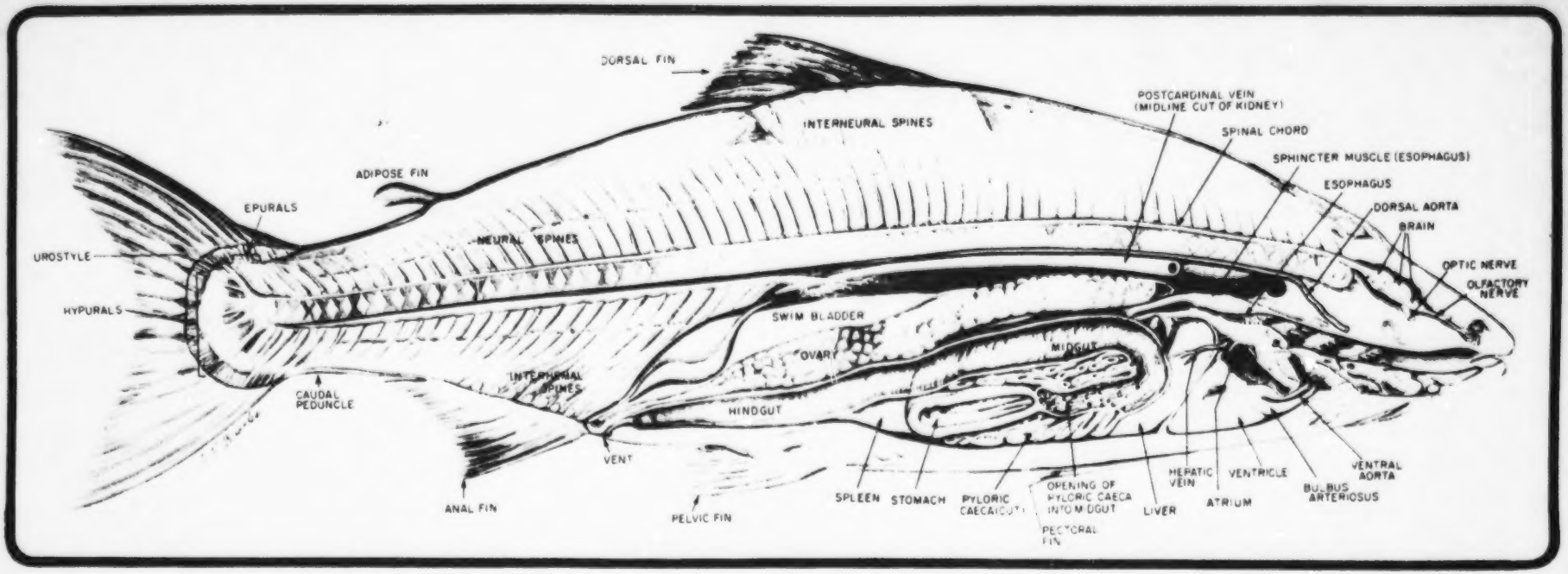


FIG. 2. Semi-diagrammatic drawing of a sagittal section of an adult, female salmon showing the location and identity of further external and internal features, particularly the bones.

directly to the vent. The gonads are dorsal and lateral, apparently connecting to the urogenital papilla, as does the urinary bladder formed from the union of the paired mesonephric ducts. The vertebral column is large and straight to carry the compression loads of the substantial musculature found in these strong-swimming fish. In general, salmonids are classed as moderately primitive teleosts, largely unspecialized except for features needed in the sustained and rapid swimming, which they exhibit as part of their migratory and predatory (usually) behavior.

Figures 3, 4, and 5 show various other details of gross anatomy. Figure 3A is a ventral view of the area around the urogenital papilla, showing the collecting ducts on the ventral surface of the kidney and how the urinary bladder passes around the swim-bladder. Most salmonids have the urinary bladder on the right-hand side of the median plane, but sometimes it occurs on the left, depending perhaps upon the species or sex. (Anatomic variation does occur in many animals without apparent functional impairment.) Other than left or right, however, the anatomy of the urinary system of most species of salmonids is basically the same. Figure 3B is a lateral view of the same region after a retrograde injection of X-ray contrast medium. The urinary bladder, the ducts on the ventral surface of the kidney, and some very tiny ducts passing dorsally into the kidney are all visible. It is possible to collect urine by catheterization of the urinary bladder of captive salmon (Smith and Bell 1967; Klontz and Smith 1968).

Some details of the brain, cranial nerves and semicircular canals (organs of balance and hearing) are shown in Fig. 4 and 5A. The brain lobes are typical of unspecialized teleosts, but identification of the cranial nerves presented some difficulties. They had a number of branchings, fusions, and other problems of determining their origin, so that the names shown in Fig. 4 should be regarded as somewhat tentative. However, the main purpose of the drawings is to illustrate the general morphology of the brain and its relationship to the semicircular canals, otoliths, and pituitary gland — the last two being parts that fisheries biologists sometimes need to locate and remove from fish. The pituitary gland (hypophysis), which consists of several biochemically and histologically distinct lobes, can be obtained by exposing the base of the brain through the roof of the mouth (the route used for hypophysectomy) on the median plane just posterior to the dorsal attachment of the first gill bar. But a more convenient technique for collecting pituitaries from a large number of adult salmon was described by Tsuyuki et al. (1964); this involves coring out the whole brain area from the top surface of the head through to the gill arches and then excising the nearly pea-sized gland following a knife cut across the core. The two large otoliths (sagittae) are often obtained by cleaving the head in half vertically from head to tail (a sagittal section), or sometimes by cutting the head transversely just posterior to the brain. Alternatively, the sagittae can be removed from beneath the posterior end of the cranial cavity near the median plan using the punch developed by McKern and Horton (1970). The openings in the bone through which the horizontal semicircular canal passes are shown in Fig. 5B for further orientation.

Bilton and Jenkinson (1968) found that the scale and otolith methods for aging sockeye and chum salmon gave comparable results, and they discussed the advantages and disadvantages of these methods.

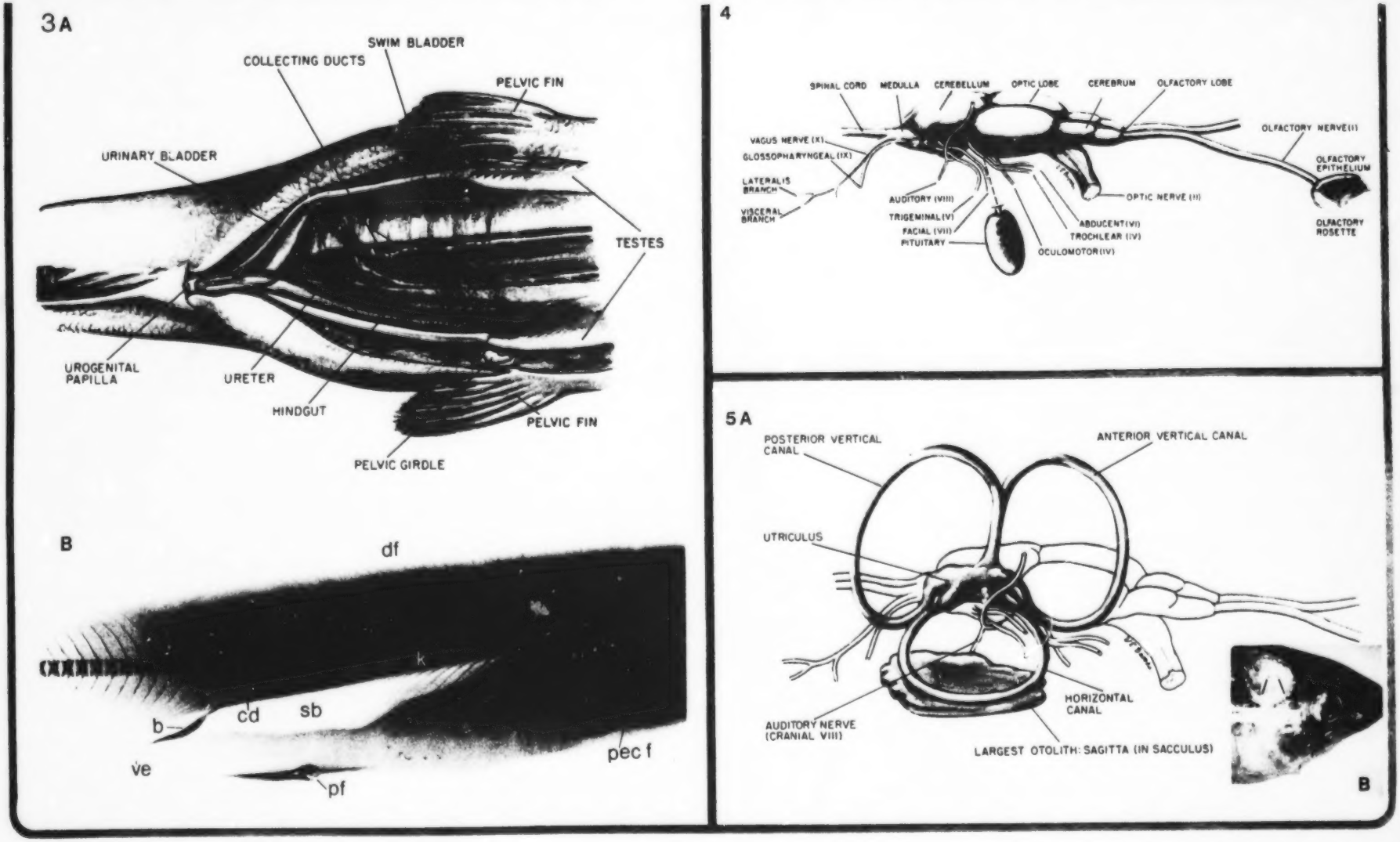


FIG. 3. The urogenital system. A, Semi-diagrammatic drawing of the ventral aspect of a male salmon showing the collecting ducts on the surface of the kidney leading to the urinary bladder that opens at the urogenital papilla; B, Print of an angiogram of the right side of a live salmon that has been injected up the urogenital opening with contrast medium. The urinary bladder shows to the left and the draining ducts on and into the kidney show immediately above the white swimbladder. The image is reversed, contrary to radiological custom, so that the filled vessels are more obvious, e.g. on the original film the blood vessels and bones showed as light areas and the swimbladder and other air spaces, or less dense areas, were dark. (Abbreviations: b, urinary bladder; cd, collecting ducts; df, dorsal fin; k, kidney; pf, pelvic fin; pec f, pectoral fin; sb, swimbladder; ve, vent.)

FIG. 4. Semi-diagrammatic drawing (uniform scale) of the brain, certain nerves (named adjectivally and numbered according to convention), and the excised pituitary (hypophysis). The actual location of the pituitary is indicated by the dotted line.

FIG. 5. Semicircular canals. A, Semi-diagrammatic drawing (uniform scale) of the right set of semicircular canals of a salmon showing its spacial relation to the brain and principal otolith. The horizontal canal has been bent downward for illustration and would actually be perpendicular to the plane of the page. (Sacculus not illustrated.); B, Photograph of the head of a salmon in which a part has been cut away to reveal the two openings in the cartilage (see pointers) through which the horizontal canal loops.

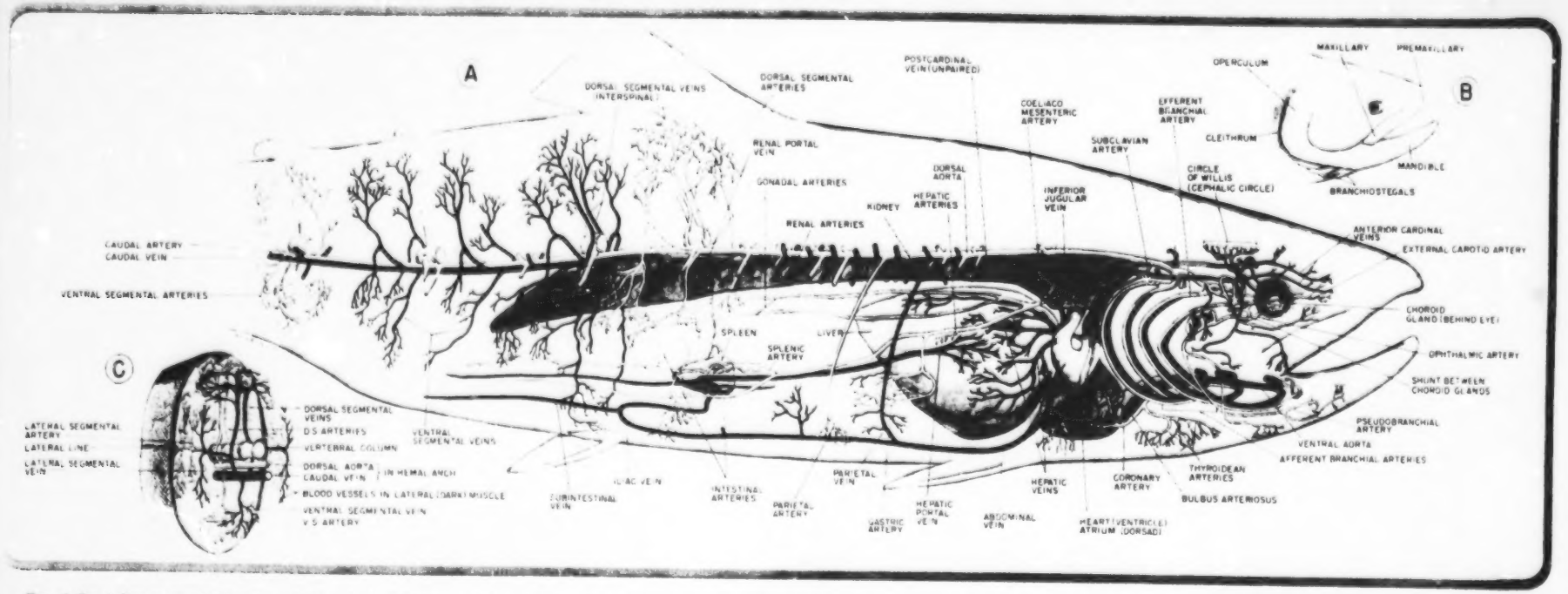


FIG. 6. Semi-diagrammatic drawing of the principal features of the cardiovascular system of salmon (A and C) and some external details of the head (B). These drawings should be used as a guide for the identification of certain anatomic features shown but not necessarily named in subsequent illustrations.

CARDIOVASCULAR AND LYMPHATIC SYSTEMS

Figure 6A is a semi-diagrammatic representation of a typical cardiovascular system of salmon, and Fig. 6B and C show features of the head, and details of the vascularization in a posterior section of muscle, respectively. Most of these illustrations are self-explanatory, but several special features are discussed in detail later. Photographs of corrosion casts of a salmon blood-vascular system such as Fig. 7 and 8 will give some appreciation of the extent and complexity of the actual system although these are by no means complete casts. For example, peripheral capillary beds that would otherwise obscure the main vessels were not filled with plastic, and many segmental veins had broken off. Generally, casts of veins appeared larger and flatter (ovoid cross section) than comparable arteries, and the segmental veins were especially prone to breaking off at the base. Also, the segmental veins have short, smooth knobs scattered along their length. Figure 9A and B show the principal arterial system and portions of the venous system of living salmon in relation to the skeletal structure and other body features. Significant portions of the blood system are illustrated in Fig. 10 where one can see the substantial nature of the hepatic vein with its extensive arborization (A); the ventral aorta as it is on the floor of the mouth (B); certain afferent and efferent cardiac vessels in situ (C and D); a cast of the relatively large (cf. to kidney) post-cardinal vein (E), and a cast showing the pattern of peripheral circulation (F).

Figure 11 is an attempt to generalize and simplify even further than in Fig. 6A. There are three major kinds of circuits through the body after blood leaves the gills. One type of flow pattern involves blood passing through capillaries in skeletal muscle or visceral organs and then going through a portal system, either renal or hepatic. A second type involves those branches of the dorsal aorta that pass through a capillary bed, but return directly to somewhere near the heart without passing through a portal system, e.g. segmental vessels anterior to the caudal vein and vessels from the pectoral girdle. Third, there are a number of specialized vessels in the head region that arise directly from the efferent branchial arches rather than from the dorsal aorta. These include the coronary (hypobranchial) artery, the afferent pseudobranchial artery, opercular artery, and the orbital artery. There may possibly be combinations of these types, e.g. in the region of the visceral cavity, the ventral segmental veins clearly connect to the abdominal vein and then return directly to the heart; the lateral segmental veins enter the kidney mass, but it was not clear in our preparations whether they connect directly to the posterior vena cava inside the kidney or pass through the renal portal system first and then into the post cava. Work on *O. mason* showed a renal portal system existing between the parietal veins and the postcardinal vein (Leenheer 1969). The functional importance of knowing the prior history of blood in a given vessel is that if the blood is leaving an organ served by a portal system, it is particularly low in oxygen and pressure as compared to blood having passed through only a single capillary bed.

The lymphatic system was not a particular subject of our investigations, but what is thought to be a major lymph vessel appeared in some angiograms, and was also seen during dissections. Presumably this dorsal lymph vessel was filled with radiopaque medium antero-posteriorly but functionally drains anteriorly, since the vessel tapered down and finally disappeared near the anterior end of the dorsal fin (Fig. 9B). This vessel has been seen in only five of many corrosion preparations, and in three of five casts, this "lymphatic" vessel system was almost devoid of the particulate red pigment

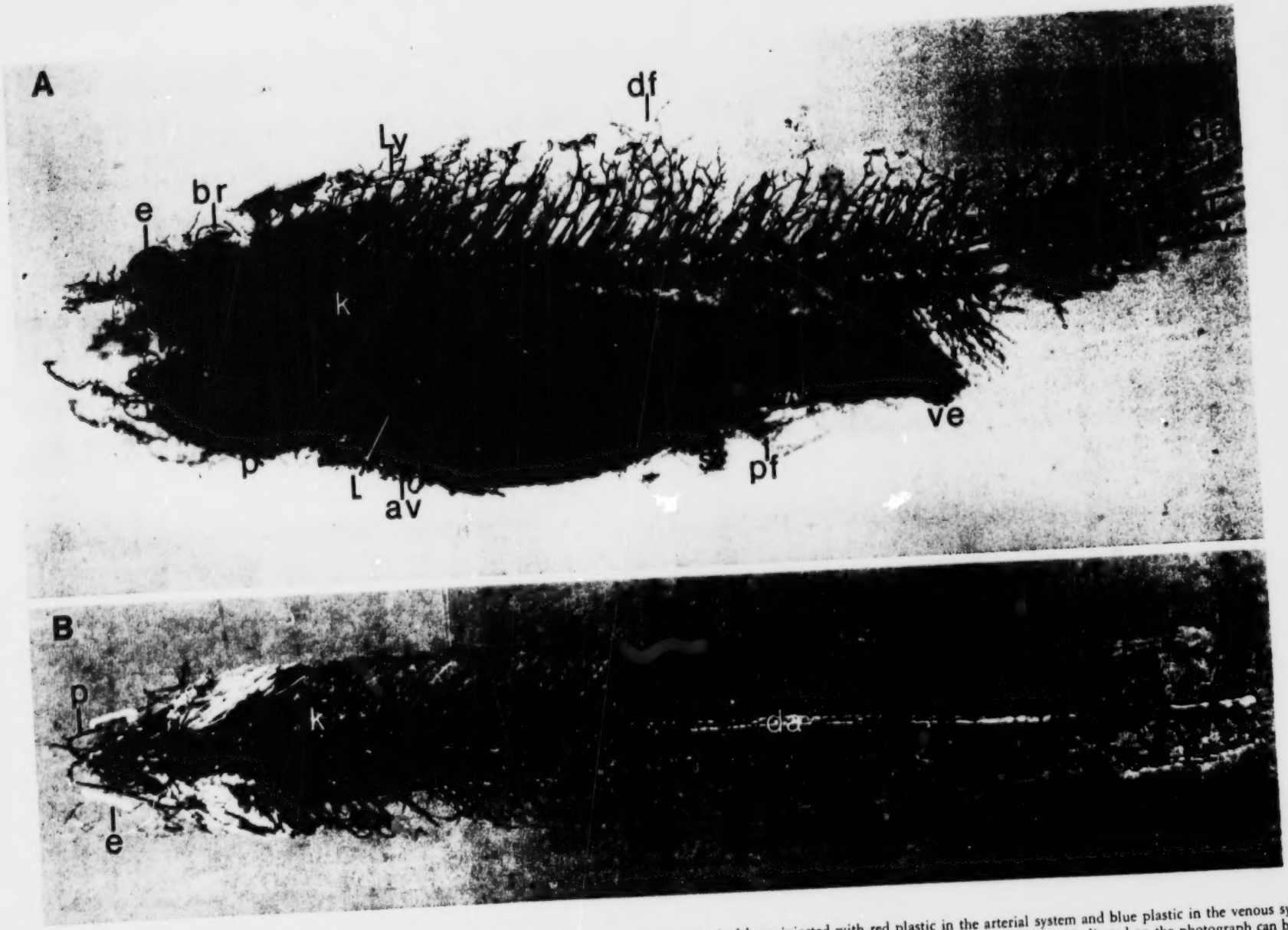


FIG. 7. Photographs of corrosion casts of the cardiovascular system of two ca. 40-cm male sockeye salmon that had been injected with red plastic in the arterial system and blue plastic in the venous system. (For some reason the heads received little or no blue plastic.) A, The left side to show especially the liver and spleen. Identification of other organs and vessels not indicated on the photograph can best be made by reference to Fig. 6. The dorsal aorta and caudal vein actually run contiguously but have become separated during preparation of the specimen; B, Dorsal view of another salmon showing the pattern and shape of the segmental arteries and veins. (Abbreviations: av, abdominal vein; br, brain capillaries; cv, caudal vein; da, dorsal aorta; df, dorsal fin; e, eye socket; g, gill arches; k, kidney; l, liver; ly, lymphatic vessel (?); p, pseudobranchial artery; pf, pelvic fin; s, spleen and ve, vent.)

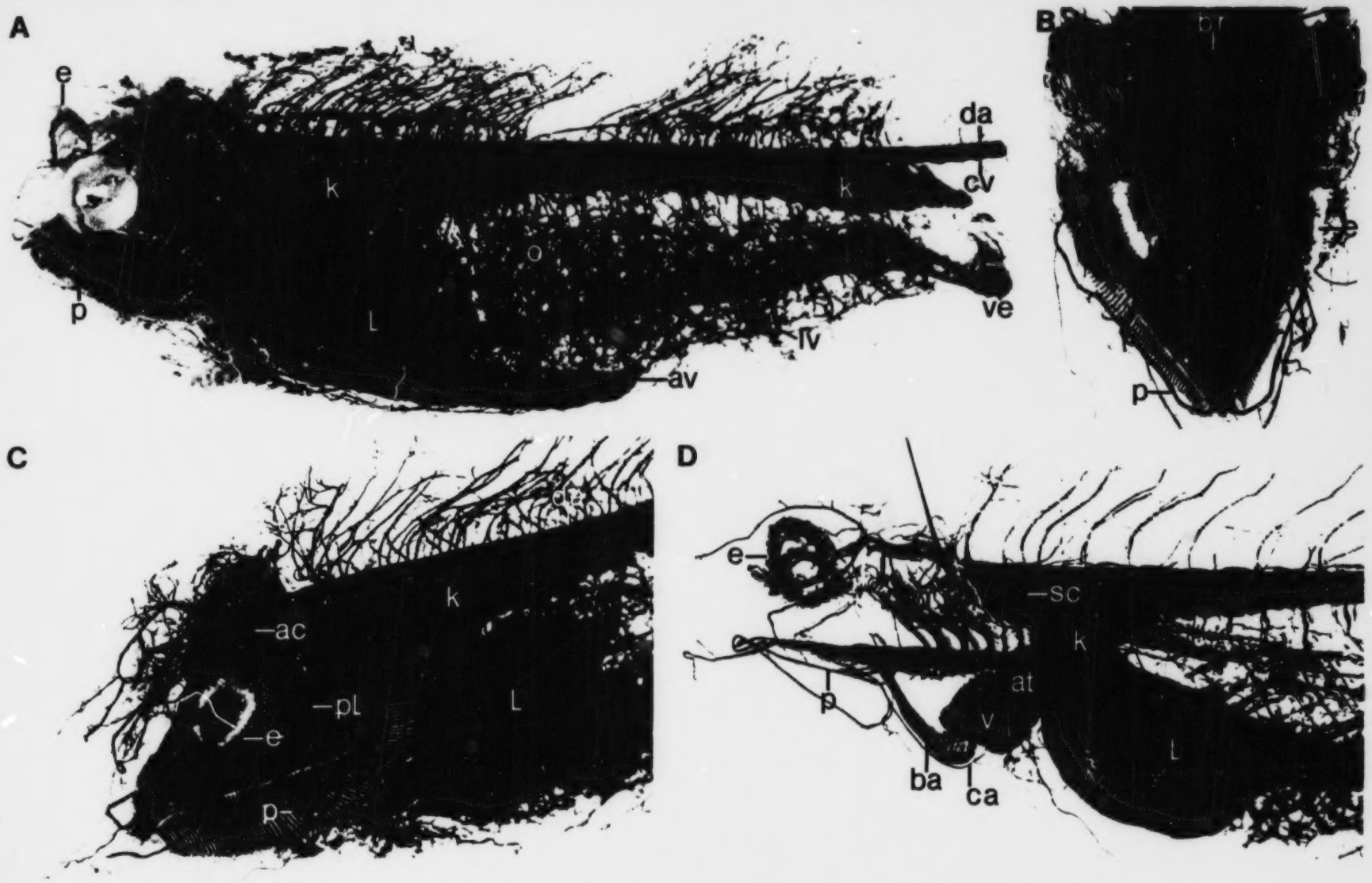


FIG. 8. Photographs of corrosion casts of the cardiovascular system of ca. 30–35-cm sockeye salmon injected with red plastic in the arterial system and blue plastic in the venous system. Identifying symbols have been minimized so as not to hinder examination of the systems: see previous figures for details. A, A somewhat bleached cast of a female fish showing the vascularized network of the maturing ovaries and of the eye "cups" (choroid gland). Note the two substantial parietal veins connecting the kidney, abdominal vein and subintestinal vein; B, Dorsal view, head pointing down, of a male fish showing the anterior cardinal veins (paired, blue) some of which drain from the area of the choroid gland; C, Semi-lateral view of the specimen shown in Fig. 8B (some pieces of plastic have broken off the liver); D, A pruned cast showing especially the gill arches (g), a lobe of the anterior (hemopoietic) kidney descending over the liver (mottled), the chambers of the heart, the subclavian (sc) and coronary arteries (ca). The straight, brown line at the top of the photograph is a supporting hook, and the artery descending nearly vertically at the bottom of the photograph has been bent out of position. (Male). (Abbreviations: ac, anterior cardinals; at, atrium; av, abdominal vein; ba, bulbus arteriosus; br, brain capillaries; ca, coronary artery; cv, caudal vein; da, dorsal aorta; e, eye socket; g, gill arches; iv, iliac vein; k, kidney; l, liver; o, ovarian system; p, pseudobranchial artery; pl, pseudobranch lamellae; sc, subclavian artery; v, ventricle and ve, vent.)

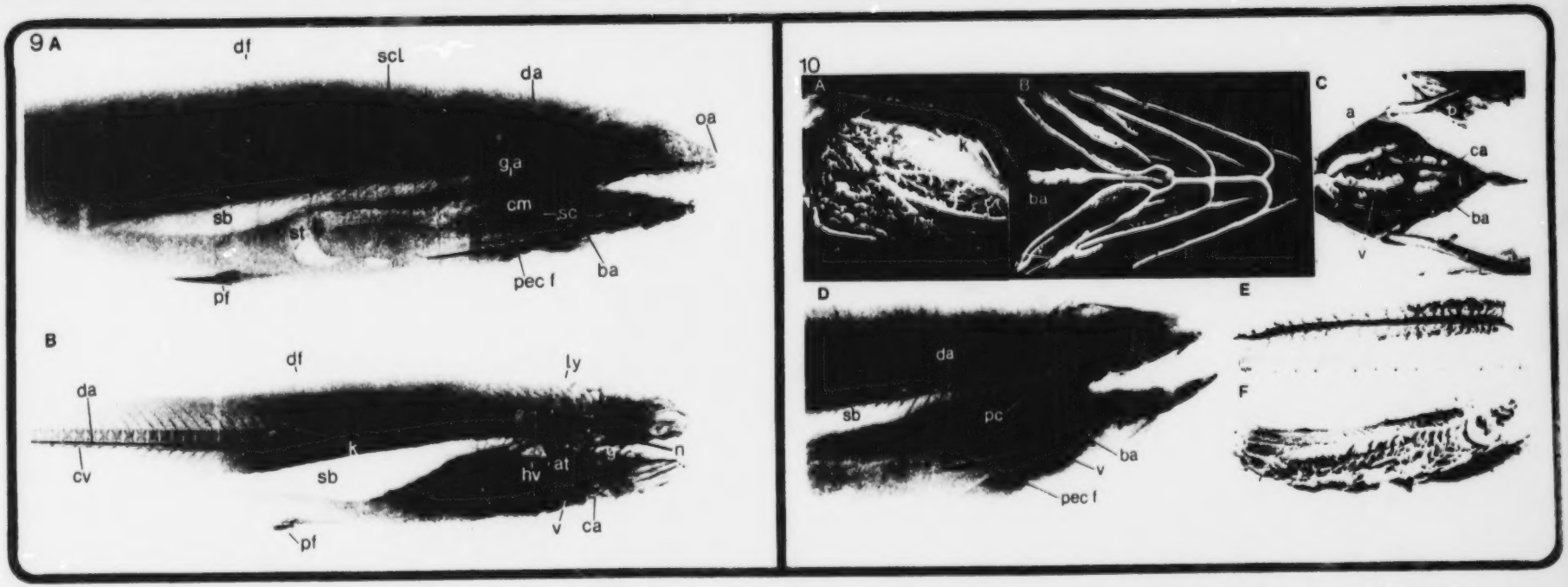


FIG. 9. Prints of angiograms of living salmon: blood vessels show as continuous dark lines or solid areas, and air spaces show as light areas. Very fine blood vessels can sometimes be confused with bones unless the angiogram is carefully examined. A, A wild caught coho showing the main arterial system in relation to the bone structure, swimbladder (sb) and stomach (st). Note the small fish in the stomach: head near the "st" and body curved around the loop leading to the lower intestine; B, A cultured sockeye that had been injected with contrast medium via a cannula and needle (n) implanted in the dorsal aorta at the roof of the mouth. The sinus venosus and atrium (at) show as a dark area just to the right of the hepatic vein. The renal portal system appears as arborizations arising from the caudal vein (cv) where it enters the posterior portion of the kidney. Diffuse, dark areas in other parts of the kidney are probably renal arteries branching from the dorsal aorta. (Abbreviations: at, atrium; ba, bulbus arteriosus; ca, coronary artery; cm, coeliacomesenteric artery; cv, caudal vein; da, dorsal aorta, df, dorsal fin; ga, gonadal artery; hv, hepatic vein; k, kidney; ly, a lymphatic vessel (assumed); n, needle; oa, olfactory arteries; pf, pelvic fin; pec f, pectoral fin; sb, swimbladder; sc, subclavian artery; scl, spinal column; st, stomach; and v, ventricle.)

FIG. 10. Additional features of the cardiovascular system. A, Corrosion cast of the left side of a partly digested adult sockeye showing the hepatic veins. The "L" shaped structure in the lower left corner is part of the abdominal vein; B, An isolated cast of the ventral aorta, bulbus arteriosus (ba) to the left and the anterior aspect to the right; C, Ventral view of the exposed heart of a plastic-injected, undigested salmon showing the plastic-filled auricle (a) of the atrium, a naturally soft portion of the heart; the muscular ventricle (v); the tough, white bulbus arteriosus (ba) and the coronary artery (ca). The branchiostegals showing under the forceps are indicated by the letter b; D, Angiogram to show the ventricle (v), bulbus arteriosus (ba) but particularly the anterior portion of the postcardinal vein (pc); E, An isolated cast of the postcardinal vein and its arborizations: ventral view, anterior aspect on the right; F, Intact corrosion cast of an adult sockeye (some bones remain) to show especially the heavy vascularization of the posterior area and the way in which the capillary beds follow the double V's of the muscle myomeres (arrow). (Abbreviations: a, auricle; b, branchiostegals; ba, bulbus arteriosus; ca, coronary artery; da, dorsal aorta; pc, postcardinal vein; pec f, pectoral fin; sb, swimbladder and v, ventricle.)

used for artery injection. This conspicuous feature suggests that the vessel was at least different from arteries and veins, but the fact that the vessel appeared to be associated with the arterial rather than venous system suggests that it might not be a lymphatic vessel. The apparent association might, however, be due to an artifact of injection. The vessel itself lies along the median plane and runs parallel to the spine, having arisen from the apex of a vertical Gothic arch (standing contiguously with arteries), lying just posterior to the brain case, the bases of which ramify around the bilaterally located thymus tissue. The location of the possible lymph vessels agrees with that stated by Harmer and Shipley (1904) when they characterized salmonids as having peripheral lymphatic systems in contrast to most other teleosts in which the main lymph vessel is axial, just above the nerve cord.

Our information on the lymphatic system is obviously incomplete but in unpublished studies of the lymphatic system of trout alevins and fry, A. D. Welander (personal communication) found both dorsal and lateral lymph ducts (vas longitudinale dorsale and truncus lateralis) and, in addition, found a ventral lymph duct and highly branched ducts in the head (vas longitudinale ventrale and truncus jugularis), only some of which were visible in our preparations.

One of us (L.S.S.) has seen a vessel that is probably a lateral lymph duct: the whole system was visible through the skin without any dissection. In 30 mm long chinook salmon used in decompression studies there was a tree-like series of vessels filled with gas in which the trunk followed the lateral line closely and the branches extended dorsally and ventrally, following the pattern of the myosepta. The branches tapered to a smaller size further away from the midlateral duct, suggesting that fluid flowed toward the main duct and thence toward the head.

The lymphatic system also has vessels draining the gill filaments, while the entire lymphatic system has multiple connections to the venous system (Dr D. J.

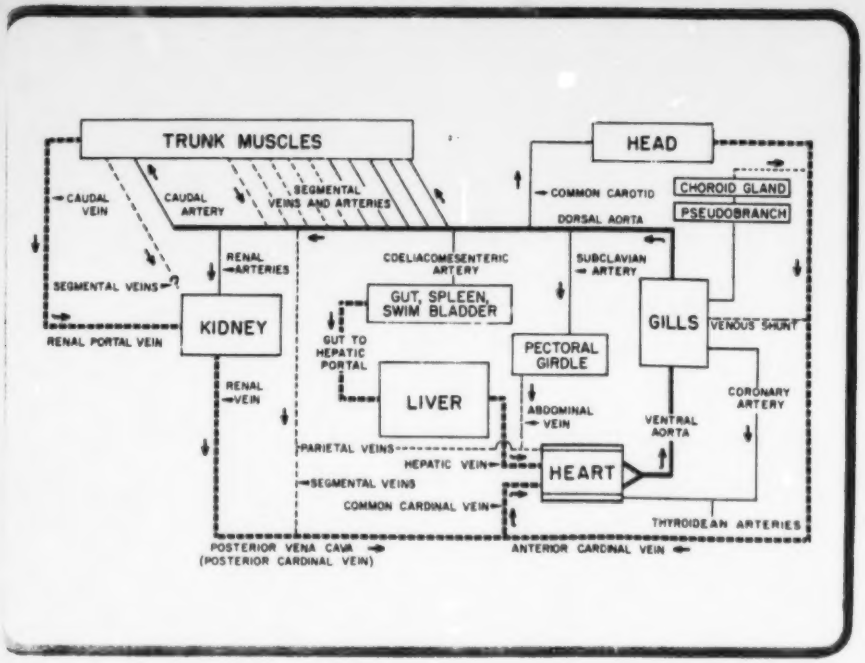


FIG. 11. A schematic illustration of the cardiovascular system in salmon giving major pathways of blood flow. Arteries are indicated by solid lines, and veins by dotted lines.

Randall, personal communication). It is common among vertebrates for the lymphatic system to be smaller in adult than in immature individuals, so it would not be surprising to find at least remnants of it in adult salmon.

KIDNEY

General features — The kidney, or actually an incompletely fused pair of kidneys, is a mass of tissue resembling clotted blood that lies along the length of the dorsal surface of the body cavity below the spine (Fig. 6A). The area of incomplete fusion, noticeably in juvenile salmon, is the so-called head kidney (pronephros) that splays out laterally over the pharyngeal region like an arrowhead (Fig. 8D). There is a gradual transition from the purely hemopoietic (hematopoietic) tissue of the head kidney to the blood filtering tissue, characterized by nephrons, of the mid to posterior portion where the urine is collected by a pair of ducts running along the ventral surface of the kidney and joining at the ureter (Fig. 3). But hemopoietic tissue can be scattered throughout, and again may be concentrated in the posterior wedge-shaped end of the kidney. On the ventral surface of the mid to posterior portion of the kidney there are usually one, two, or rarely more small whitish bodies. These are the corpuscles of Stannius, thought to serve as endocrine glands for the regulation of calcium metabolism, especially in fresh water, and also to serve in general osmoregulation. The corpuscles of Stannius appear comparable in function to the parathyroid gland of mammals but production of analagous hormones has not been demonstrated in these corpuscles. There are no discrete adrenal glands in salmon but there is adrenal tissue, including interrenal tissue that secretes steroid hormones such as cortisol, and chromaffin cells that produce adrenalin. This tissue is scattered throughout the anterior part of the kidney, especially near the postcardinal vein (Johnson 1973).

Blood supply — The filtration or blood purification function of the kidney depends upon the flow of arterial blood, and the efficiency of resorption depends upon the presence of a large pool of venous blood to minimize diffusion gradients and back-diffusion from the urine. There are many small renal arteries coming off the dorsal aorta as it passes dorsal to the kidney (Fig. 9B), and from the segmental and intercostal arteries as they pass down the body wall from the dorsal aorta (Fig. 6A).

Venous blood passes into the kidney from the caudal, segmental, intercostal, parietal and perhaps some anterior veins, but the caudal vein that drains the tail region and enters the posterior end of the kidney out of the hemal arch (see Glossary) arborizes into the main renal portal system of capillaries and sinusoids linked to the posterior portion of the postcardinal vein (Fig. 6A and 9B). All of the venous blood then returns to the heart at the sinus venosus via the postcardinal vein (Fig. 10D) that runs centrally (along the median plane) until it emerges anteriorly from the right lobe of the kidney (Fig. 6A). This system is shown schematically in Fig. 11.

HEART AND GILLS

The heart consists of a series of four grossly distinguishable chambers with a valve system that prevents backflow of blood entering this pump. Blood, principally from the postcardinal, common cardinal and hepatic veins, empties into (afferent flow) the right- or left-hand duct of Cuvier on the dorsal aspect of the heart. It is then pumped sequentially through the three contractile chambers — the sinus venosus, atrium (with its auricles), and ventricle — through and out of (efferent flows) the bulbus arteriosus (Fig. 8D). Then arteries branch from the ventral aorta (Fig. 10B) to distribute venous blood to the eight gill arches. Blood passes through vessels in the cartilaginous arches, into the filaments, and finally into the secondary lamellae where, across a ca. 3/1000 mm thick cellular membrane, oxygen is extracted from and carbon dioxide is released into the water. This water is being pumped unidirectionally (anterior to posterior) through the buccal cavity, and generally countercurrent to the direction of blood flow for efficient exchange of substances, by the combined action of the opercula and the buccal valves. The gills also act as excretory and osmoregulatory organs for the removal of ammonia (as ammonium ion in the blood), exchange of water, and for general ionic exchange.

THYMUS AND THYROID TISSUES

Thymus tissue (a discrete gland in man) occurs as irregular masses of soft tissue around the pharyngeal area near the anterior end of the head kidney and can often be seen beneath the skin where the operculum joins the body dorsally. It is tentatively assumed, mostly from mammalian studies, that this tissue helps to initiate immune processes in the young fish, produces some types of white blood cells (leucocytes) and then essentially disappears in the adult. However, such homologies must be assumed with great caution until more is known about salmon.

Thyroid tissue, which produces metabolism-regulating hormones, is not a discrete endocrine gland as in mammals but occurs as follicles scattered usually around the area of the median ventral aorta. Follicles might possibly also occur in the head kidney and choroid gland (Fig. 6A) of the eye (Gorbman 1969) in some species, although this is not likely in salmon (Hoar 1939; Hoar and Bell 1950).

Pseudobranch and Choroid Gland

The functions of the pseudobranch and the choroid gland (its glandular function is questionable) in teleosts have been widely speculated upon for many years. Recent evidence favors suggestions that the pseudobranch contains an oxygen sensor and influences blood flow in the gills (Davis 1971). The choroid gland with its dense capillary bed *(rete mirabile)* has been implicated in the production of supersaturated oxygen levels in the eye fluids (Hoffert et al. 1971). Both of these functions can be supported by the anatomic findings. First, the artery to the pseudobranch arises in the ventral portion of the first (numbering anteriorly to posteriorly) gill arch, travels anteriorly to the tip of the gill bar, then loops into the mandible and returns along the inside of the operculum until it reaches the pseudobranch (Fig. 6A; 8B and C). The efferent blood vessel from the pseudobranch (ophthalmic artery) goes to the choroid gland at the back of the eyeball. The ophthalmic arteries from the two sides are connected by an anastomosis, apparently assuring a blood supply to both choroid glands, even if the vessel on one side is damaged or obstructed. Perhaps the pseudobranch actually has some respiratory function (less likely in fish having a membrane covering the pseudobranch), maximizing or guaranteeing the oxygen content of the blood supplying the choroid gland. It could also have some function in ion exchange or pH regulation of intraocular fluids.

It is noteworthy that several diseases of salmonids produce a pop-eyed effect (exophthalmia). It is possible this results from some malfunction in the choroid gland or the venous drainage of the area behind the eye (Fig. 8B and C), leading to accumulation of fluid there.

Blood Supply to Skeletal Muscles

The functions of white and dark (lateral) muscle tissues in fish are widely accepted: dark muscle is for relatively slow, sustained swimming and white muscle is for burst swimming lasting no more than 20 s. Energy release in dark muscle is largely aerobic, that in white muscle largely anaerobic. It is not surprising that the blood circulation reflects this difference, but the degree of difference seen in the corrosion preparations was much greater than we expected. The lateral muscle contained a great profusion of capillaries, while the white muscle contained fewer. With so little perfusion of white muscle, it is no wonder that repayment of an oxygen debt, involving oxidation of lactate, requires up to 24 h.

The capillary bed of the lateral muscle appeared rich near the caudal fin but became more sparse anteriorly (Fig. 10F). It is possible that this phenomenon resulted from most injections being made caudally and pressure being greatest there, but it also fits the functional hypothesis that the greatest muscular activity occurs posteriorly.

Sites for Repeated Blood Sampling or for Injection

If killing the fish is acceptable, or if its small size gives no alternative, then the easiest way to get blood is to cut off the tail. This method will give mixed arterial and venous blood but is satisfactory for many routine tests. However, when it is necessary to obtain, non-destructively, a blood sample from a salmonid, some knowledge of the cardiovascular anatomy is required. The possibilities of various sampling or injection sites can best be assessed by consulting Fig. 6. Three commonly used sites for sampling or injection are given first below, followed by five other potentially useful sites, the choice depending upon the requirements of the project, e.g. type of blood, frequency of sampling, part of the fish to be monitored, and duration of the experiment.

Anterior Dorsal Aorta

Samples from anesthetized fish (about 200 g or more) may be obtained conveniently by inserting the needle of a hypodermic syringe at an angle of about 40° to the roof of the mouth at a central point (on the median plane) between the third and fourth gill arch at the back of the mouth until it touches bone (Fig. 9B). Small-mouthed fishes may be more conveniently bled by entering the dorsal aorta from a point just anterior to the first gill arch and on the median plane, with the syringe almost parallel to the roof of the mouth. A tuberculin-type syringe is ideal for this. These techniques were devised by Schiffman (1959) and modified by Smith and Bell (1964) so that repeated blood samples could be taken without having to anesthetize the fish each time. One should avoid damaging or obstructing the first gill arch to prevent restriction of the blood supply to the head. The dorsal aorta is a good site from which to obtain well oxygenated, arterial blood with a minimum of damage to the fish.

Ventricle

A ventricular puncture is made at the junction of the midventral line (linea alba) with a line drawn across the anterior-most insertion of the pectoral fins. Angling the needle about 20° posteriorly from the vertical at this point usually results in penetration of the posterior part of the ventricle (Fig. 9B and 10C). This site is readily accessible and has been used successfully by a number of investigators. It might pose some problems through damage to the coronary blood supply, the thyroid blood supply (Fig. 6A), the inner surface of the ventricle — as it moves against the sharp edge of the needle, or to the pericardial space by filling it with blood and thereby stopping the heart. In spite of these possible problems, investigators who chose this site have taken weekly blood samples from the same fish without apparent harm for over a year. The method works best on larger fish and is a good site to obtain well-mixed venous blood.

Caudal Vein

This vessel is routinely approached on the midventral line posterior to the anal fin. The needle is inserted at right angles to the side and the blood vessel entered by probing for the space between the hemal arches. This is the least damaging of the three sites for such probing, but it has other problems. The caudal vein lies immediately ventral to and partly surrounding the dorsal aorta (caudal artery) and sometimes the needle penetrates both vessels. Interpretation of the blood sample could then be difficult if a venous vs. arterial distinction were required. Cannulae have also been inserted here through hypodermic needles or trochars.

Material injected into the caudal vein must pass through the kidney before reaching the rest of the body. If the injection material were of a nature to be influenced (cleared, excreted, metabolized) by the kidney, then this fact could be either useful or disadvantageous depending on the experimental objectives.

Efferent Branchial Artery

Blood can usually be obtained by inserting a hypodermic needle parallel to a gill bar at a shallow angle along the base of the gill filaments. This site is relatively convenient to reach by lifting up the operculum and inserting the needle toward the midline. One obtains oxygenated (arterial) blood reliably if far enough dorsal so

that the afferent branchial artery is small. The site could be a good alternative to that of the dorsal aorta, although the precaution of avoiding the first gill arch is much the same as for sampling in the dorsal aorta because of possible interference with the blood supply to the cranial area.

Common Cardinal Vein

The common cardinal vein is a fusion of the anterior and posterior cardinal veins that occurs only on the right side of the fish (Fig. 6A). It lies close to the surface beneath the cleithrum (Fig. 6B) and is large enough to be found easily by probing with a needle at an 80° angle to the side of the fish just dorsad to the lateral line behind the bony cleithrum: blood wells readily into the syringe. One possible difficulty in the use of this apparently new-found site is its nearness to the hepatic veins, and the contribution from these vessels might be quite variable. But this would also be similarly true with blood from the ventricle. This site warrants further investigation.[1]

Ventral Aorta

Although attempts to cannulate the ventral aorta via a midventral incision through the muscles of the isthmus all failed, this potentially convenient site, particularly for single samples, still appears to need further investigation. There were problems initially with blood leaking around the incision in the wall of the aorta where the cannula entered, but the fish died within a few hours, even after bleeding was minimized. The obvious problem of cutting the coronary artery where it lies on the ventral surface of the ventral aorta (Fig. 6A) was avoided. It was not until corrosion preparations were completed that the additional branch of the coronary (hypobranchial) artery was found (Fig. 6A) that supplies the muscles of the isthmus and probably the thyroid follicles as well. Complications produced by interference with this blood supply in making a midventral incision presumably caused the delayed mortalities observed earlier and would need to be considered in any further investigations into this sampling site. Some investigators apparently enter the needle via the ventral aorta from inside the mouth under the anterior end of the tongue.

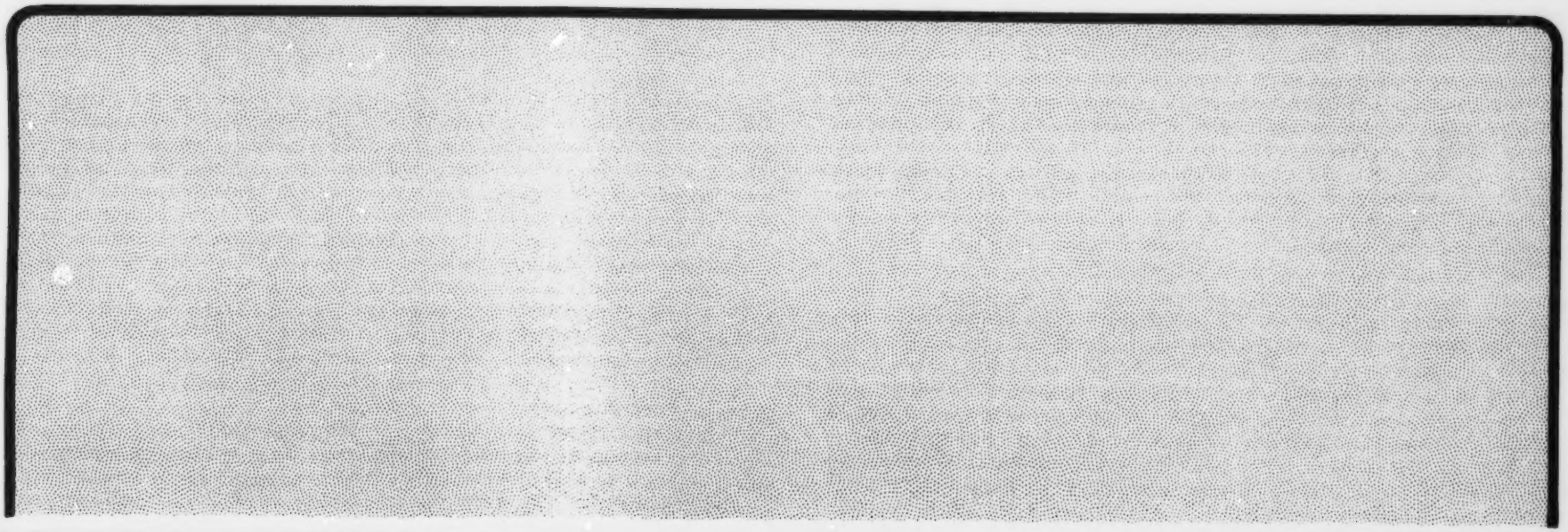
Abdominal Vein

In fish of about 45 cm or larger the abdominal vein that runs midventrally near the surface of the belly (Fig. 6A and 7A) might also be used. Finding the vessel is the major difficulty and would probably require a type of celiotomy, i.e. exposure by means of a small, carefully made incision running between the pectoral and pelvic fins. But perhaps infrared, electromagnetic or acoustic principles could be used to locate the vessel.

Other Sites

One of the sites we used for rapid uptake of injected material when it was inconvenient or undesirable to enter a blood vessel, was along the dorsal midline, preferably just anterior or posterior to the dorsal fin. Material thus injected into the space around the neural spines did not ooze back out of the needle puncture, and uptake occurred in a few hours (presumably due to the presence of the dorsal and other lymphatic ducts). Injections into the deep muscles give slow dose dissemination and usually result in appreciable loss of material from the site. Intraperitoneal injections also result in relatively slow uptake, an advantage in administering toxic substances or if longer term "physiological" dosing is required (e.g. vaccination), and there is little or no loss of material from the site.

[1]Added in proof: blood sampling via the duct of Cuvier (see common cardinal vein) — Lied, E., J. Gjerde, and O. R. Braekkan. 1975. Simple and rapid technique for repeated blood sampling in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 699–701.



Glossary of Terms

Afferent — leading or flowing into a named body or area, e.g. the afferent branchial artery brings blood into the gills from the ventral aorta.

Anastomosis — a natural, functional communication between two blood vessels or other tubes.

Anterior — the head or front end of the animal.

Aorta — a large, elastic artery of the main trunk of the arterial system.

Artery — a thick-walled, elastic vessel conveying blood, usually bright red and well-oxygenated, away from the heart. The ventral aorta, like the pulmonary artery in humans, carries poorly oxygenated blood.

Autonomic — in reference to a nervous system denotes functional independence from external or cerebrospinal influence: controlling glands and smooth muscles.

Branchial — relating to the gills.

Celio, celo, coel — prefixes (usually) indicating some relationship to the abdomen, belly, or body cavity.

Cross plane (transverse plane) — a vertical section across the body at right angles to the sagittal plane.

Dorsal — the top or upper side of the body. (Dorsad — toward the top or back of the fish: many other similar adverbs are made by changing the "l" to "d," e.g. caudad — toward the tail.)

Ectomy — a suffix indicating operative removal of the organ or gland named.

Efferent — leading or flowing out of a named body or area.

Gonad — the general name for a male or female sex organ, testis or ovary, respectively.

Hemal (haemal) arch — a ventral extension of the vertebrae (hemal spines) that encloses the dorsal aorta and caudal vein in bone once the vessels pass posteriorly out of the body cavity.

Hemopoietic (haemopoietic, hematopoietic) — pertaining or relating to blood cell formation.

Hepatic — relating to the liver.

Intercostal — between the ribs.

Lateral — the side of the body, left or right.

Median plane — a vertical (dorsal to ventral), longitudinal (head to tail) section that cleaves the body into almost identical right and left halves. This is also known as a sagittal plane, but not all sagittal planes or sections are necessarily median ones. See **Parasagittal**.

Parasagittal — any sagittal section parallel to the median plane.

Parietal — pertaining to the wall of a cavity, e.g. the body cavity wall.

Peripheral — the outer part or surface of a body; away from the center of the body.

Posterior (caudal) — the hind or tail end of the animal.

Portal system — a network or bed of capillaries occurring in the path of a vein or veins to facilitate blood-tissue contact within an organ, e.g. renal portal system helps to purify the blood, and the hepatic portal system brings nutrients from the digestive tract to the liver for resynthesis.

Renal — relating to the kidney.

Retrograde — moving backward.

Sagittal section or plane — see **Median plane**.

Teleost — bony, ray-finned fishes; the most flourishing and highly developed of fishes.

Vein — a thin-walled vessel carrying dark, or poorly oxygenated blood toward the heart.

Ventral — the belly or lower side of the body.

Visceral — the internal organs or soft parts within the body cavity.

Acknowledgments

A number of persons assisted in this work over the years and we gratefully acknowledge their help.

Mr Bob De Lury formerly a student worker at the Pacific Biological Station (P.B.S.) made and photographed some of the corrosion casts, and several of these were dissected by Mr Timothy Newcomb while a graduate student in the College of Fisheries, University of Washington (U. of W.).

Ms Virginia Brooks, medical illustrator of the Medical School (U. of W.), made most of the drawings and assisted in simplifying the mass of blood vessels found in most corrosion preparations. Her work and some of the photography was supported by a grant from the Graduate School Research Fund of the U. of W.

Mr A. Denbigh of the P.B.S. deserves special thanks for preparing Fig. 6, partly from an illustration by V. Brooks. Messrs E. Warneboldt and S. Dakin of Nanaimo provided valuable advice and assistance on photographic problems. Mr John Ketcheson (P.B.S.) photographed one corrosion cast (Fig. 7A): other color photographs are due to E. Warneboldt. M. J. Smart (M.B., B.S.) of Nanaimo assisted in preparing the radiograms.

Dr E. Don Stevens of the Department of Zoology, University of Hawaii, provided notes and drawings that he made while a student working at the P.B.S. Dr Arthur Welander, College of Fisheries, U. of W. assisted in our interpretation of the lymphatic system with unpublished drawings and notes of lymph vessels seen in fry, and provided useful references. Mr Rick Crickmer (deceased) assisted with dissection and interpretation of the cranial nerves while he was a graduate student in the Department of Zoology, U. of W. Mrs Mavis Colclough of P.B.S. patiently and effectively typed several versions of the manuscript from rather chaotic-looking raw material.

We are particularly grateful to Dr W. Hoar for critically reviewing the manuscript and giving valuable suggestions despite his extraordinary heavy work load. Dr L. Margolis also made helpful suggestions, particularly regarding the organization of the manuscript.

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